




# Scientific note about the negative impacts of male competition on *Epicharis albofasciata* mating

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Sexual selection theory attempts to explain how males and females interact and how mating strategies are selected across time. The intensity of sexual selection in male bees is generally related to the degree of rarity of female bees (Shuster 2009). In the mating season, males of solitary bees usually emerge a few days earlier, making females a scarce resource (Alcock et al. 1978). When the number of males capable of mating is much higher than the number of females, there is a strong competition among them (Sabino et al. 2017). This can result in fights to get the limited supply and usually leads to negative effects on the competitors (Lang and Benbow 2013).

Males of solitary bees typically search for females at flowers or at their emergence sites, and mating strategies vary widely among species (Paxton 2005; Alcock 2013). Scramble competition polygyny is a mating strategy where females are sparse in the territory, and there is

a possibility for males to compete to find them before their opponents (Alcock 2013). This is based on differences in their ability to move about and locate females. Females of solitary bees usually copulate just once (Alcock 2013). The polyandry refers to females that are inseminated by more than one male to produce brood, assuming that males generally have multiple copulations if there is opportunity (Parker and Birkhead 2012).

*Epicharis* Klug 1807 accounts for 40 species of solitary ground nesting bees restricted to the Neotropics from Mexico to Brazil (Moure et al. 2013, Rozen 2016, 2017). Information about sexual selection and mating behavior in this genus is still limited (Rocha Filho et al. 2008, Hiller and Wittmann 1994; Martins et al. 2019; Pina et al. 2020; Dec and Vivallo 2021). Here, we report, for the first time, the mating behavior of *Epicharis* (*Epicharioides*) *albofasciata* Smith 1874. We discuss whether an aggressive competition among males to access virgin females may affect the reproductive success of the species. We expected to find scramble competition polygyny, and monogamous females, according

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to previous studies in other *Epicharis* (Rocha-Filho et al. 2008; Martins et al. 2019; Pina et al. 2020; Dec and Vivallo 2021).

We studied a nesting aggregation of *E. albofasciata* at a private farm (23° 25' S, 46° 10' W) in the Atlantic Forest domain in Sao Paulo State, southeastern Brazil. The nesting site (80 m<sup>2</sup>) was established in a sandy bank close to a flooded area. The activity of the bees was observed over 3 days a week from December 5, 2014 to January 13, 2015, totaling about 90 h. Observations were performed between 07h00 and 16h00. The mating strategy was evaluated by recording short videos and marking males and females with non-toxic paint pens (Posca® — Tokyo, Japan) to identify individuals during the mating process. We looked for male patrolling, but we did not find any at aggregation site or around. As in *Epicharis dejeanii* and *E. metatarsalis*, the males patrolling for females consist in performing circular flights or eight figures around the nests (Thiele and Inouye 2007; Pina et al. 2020). Males flew searching for virgin females from 08h00 to 15h30. Peak flight activity was around 09h00, but it declined greatly on cloudy or rainy days. We recorded eight events of males inspecting the nests before female emergence; this behavior was also observed in *E. metatarsalis* (Thiele and Inouye 2007). Usually, two males observe the nest entrance, if a third male come, they start to fight. Whenever a female emerged, a cluster of up to 10 males crowded on her and started to fight to be her mate (Supplementary material). The copulation events consist of the female holding onto the substrate (leaves or soil), while the male grasps her from above alternating genital contact and protecting the female from rival males. As a defensive posture, the male keeps his front and middle legs on the female and his antennae horizontally erect. When a rival male approaches, the male raises his meso and metathoracic legs, exposing the enlarged tibial spurs, and raising his antennae to a vertical position. The males remain only in their defensive postures for approximately  $102.9 \pm 69.1$  s ( $N=7$ ; mean  $\pm$  SD). When there is no interference from rival males, a male has his first genital contact and repeatedly taps the female's head or/and

antennae with his antennae while holding her with his pro and two mesothoracic legs. Genital contacts last  $27.2 \pm 9.4$  s ( $N=8$ ), while the male vibrates his wings continuously and emits a rhythmic low frequency buzzing sound. In *Centris pallida*, the antennal taps and leg stroking is a signal that induces fidelity in the females, and they do not mate again (Alcock and Buchmann 1985).

After copulation, the pair remains in the same place for about 3 s. The male passes his hind legs along the female's abdomen and his front legs along her antennae. This behavior may reduce the attractiveness of females to other males (Ayasse et al. 2001). However, our marked females ( $N=5$ ) copulated with more than one male. In these cases, immediately after the departure of the male, a new male made genital contact with the female before she was able to groom herself or leave. It seems a case of polyandry, which is not common in *Epicharis* (Rocha-Filho et al. 2008; Martins et al. 2019; Pina et al. 2020; Dec and Vivallo 2021), even when females are placed with other males after their first mating (Dec and Vivallo 2021). Although one female of *Epicharis nigrita* was observed copulating with two males (Martins et al. 2019), we do not know whether *E. albofasciata* is truly polyandric, or the males are forcing rapid new copulations because of the intensity of the competition at the nesting site, as suggested by Alcock et al. (1978).

The intense fighting among males to access virgin females caused severe damage or even death to some females ( $N=5$ ) (Fig. 1d). For example, we observed an extreme case of the intense male competition, when a female was decapitated in the middle of the mating cluster, and the males continued copulating with the rest of her body ( $N=1$ ) (Supplementary material). Females died soon after copulating with several males ( $N=4$ ). In another situation, a female lost part of her abdomen and died after copulating with six different males ( $N=1$ ). Also, during the scramble competition, males were severely damaged, losing part of their body, had their wings cut, or died. Another intriguing behavior observed among males is to strike the females that they had previously copulated with. Although



**Fig. 1** Sequence of mating behavior of *Epicharis (Epicharioides) albofasciata*. **a** A cluster of males around a female on the ground at the nesting site. **b** Male defending a female against a rival male. **c** Mating on a leaf in which a male is grasping a female. **d** Dead female after intense competition among males to copulate with her

*Epicharis bicolor* females also form clusters with several males, they copulate just once and do not get damaged (Rocha-Filho et al. 2008).

In the bee mating literature, we did not find anything as extreme as the aggressiveness of males we observed (Alcock 2013). Different from *Epicharis picta* (Smith 1874) that has around 1:1 male to female (Werneck and Campos 2020), the population we observed may be unbalanced in its sex ratios. Intense competition among males occurs when there is asymmetry of parental investment in the sexes (Parker 1979).

More males in a population could mean that some disturbance is occurring. One hypothesis is that there might not be enough pollen resources for the production of females, since they are the more costly sex to produce. Previous studies have shown that the ratio of males increases when food availability declines (Torchio and Tepedino 1980; Kim 1999). Another possible explanation is that the previous generation was unbalanced regarding females, leading many females not to be inseminated, producing unfertilized eggs (haploid eggs) that produce males.

We believe that the aggressive behavior of *Epicharis albofasciata* males is caused by their intense competition to copulate and to be the first and only male to mate with a virgin female. The high aggressiveness of the males poses direct costs for themselves and for the females. After strong harassment and/or multiple matings, some females died, while others may not be able to construct and provision a nest. This could affect female fitness and may undermine or otherwise threaten population stability. In this *E. albofasciata* population, the extreme costs to females may affect the next generation through a decline in the number of individuals.

Supplementary information.

Video 1 The aggressive mating cluster around a pre-emerged female.

Video 2 A male copulating with a decapitated female after successive copulations.

## SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-022-00911-y>.

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## AUTHOR CONTRIBUTION

CAC, WOS, IAS, and GDC conceived this research and implemented the field data collection. The first draft of the manuscript was written by CAC. CAC, WOS, IAS, GDC, and SLB participated in the revisions. All the authors read and approved the final manuscript.

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## AVAILABILITY OF DATA AND MATERIAL

If requested, we will be happy to share photos and videos about the Scientific Note.

## CODE AVAILABILITY

Not applicable.

## DECLARATIONS

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Conflict of interest** The authors declare no competing interests.

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